

AVAILABILITY OF NESTING HABITAT MAY NOT DRIVE COLONY FORMATION
IN CHESTNUT-HEADED BEE-EATERS *MEROPS LESCHENULTI*
IN SOUTHERN INDIA

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Colonial breeding may be driven by patchy breeding habitats leading to congregation of individuals at suitable sites, or by conspecific attraction, where individuals choose to nest in the proximity of past or present nesting sites of conspecifics. The selection of habitat might also be influenced by age and body condition. Chestnut-headed Bee-eaters *Merops leschenaulti* (CHB) breed solitarily and in small colonies. Data on nesting pairs and nests were collected over five months from December 2010 to May 2011 during the breeding season in Haliyal and Karwar Forest Division, Uttara Kannada district, Karnataka. A total of 17 nests were found during the course of the study, distributed in three colonies and five solitary nesting sites. We measured and compared habitat characteristics of nests at solitary and colonial breeding sites and found no significant difference between habitat characteristics at solitary and colonial nests. We also found that colonial nesting birds were slightly larger than solitary ones. There is some evidence pointing at despotism and the role of the previous year's nest holes in CHB nesting behaviour, and further investigations are required to validate the hypothesis.

Key words: Group breeding, Conspecific attraction, tarsus length, traditional aggregation, Western Ghats

Breeding in densely distributed territories that contain no other resources apart from breeding sites is known as colonial breeding (Perrins and Birkhead 1983). Colony size shows a wide variation in many species, for example, in Bank Swallow *Riparia riparia* colony size ranges from two breeding pairs to several hundred pairs (Hoogland and Sherman 1976). This plasticity in colony size is especially remarkable, considering that there is high selection pressure on breeding behaviour (Brown *et al.* 1990; Brown and Brown 2001).

Variation in colony size, it was proposed, is a by-product of the process of colony formation involving selection of similar 'commodity' by individuals (Danchin and Wagner 1997). Habitat availability was found to be the main 'commodity' influencing the pattern of colony size variation in many species, for example, in burrowing Alcids (Kaiser and Forbes 1992) and Barn Swallow (*Hirundo rustica*) (Safran 2004). In such cases, colony formation is said to be habitat-mediated, which implies that colony size varies according to the abundance and distribution of resources (Danchin and Wagner 1997).

In many other species, colony formation is conspecific-mediated and additive aggregation of animals is observed, i.e. density of animals might be lower or higher than is expected based on habitat availability (Danchin and Wagner 1997). In such species, colonies may be maintained due to the social benefits of group breeding (Safran *et al.* 2007).

Variation in either habitat quality or quantity can influence colony formation. If variation in habitat quality is responsible for colony formation, then the habitat characteristics of sites having solitary nests must be less suitable for breeding than at colony sites. For example, Kaiser and Forbes (1992) showed that colonies of four burrow-nesting Alcids, i.e. Ancient Murrelet *Synthliboramphus antiquus*, Cassin's Auklet *Ptychoramphus aleuticus*, Rhinoceros Auklet *Cerorhinca monocerata* and Tufted Puffin *Fratercula cirrhata*, occur only on less than 2% of the 6,500 islands surveyed and 12 of the largest colonies contained about 83% of the breeding population. They found that occupied islands were located in colder, more saline water, and were subject to less intense rainfall than unoccupied islands.

However, if habitat quantity influences colony formation, i.e., there is a shortage of potential breeding sites, then all the breeding sites should be occupied up to their carrying capacity. This implies that the number of nests in a site should be proportional to the amount of substrate available, as was found to be the case in Rainbow Bee-eater *Merops ornatus* (Boland 2004).

The choice of colony size of different individuals may differ based on non-heritable variation, such as size, condition, age, experience and dominance (Ranta and Lindström 1990) or based on heritable variation (Brown and Brown 2000). In Bearded Tit, females associated with colony formation were larger and in better health condition than in

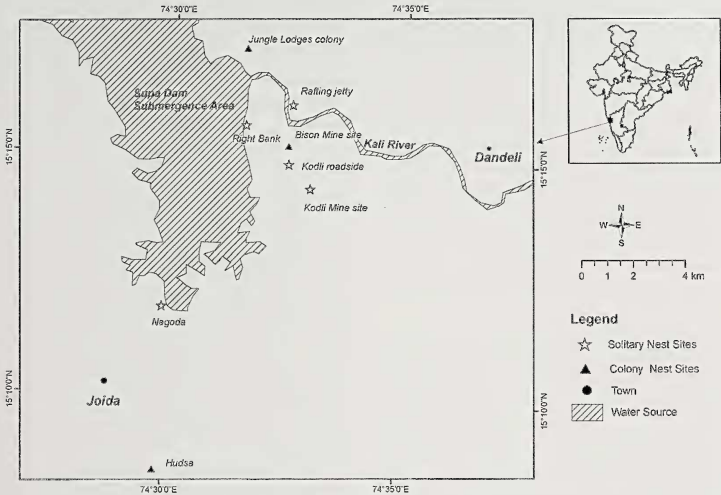


Fig. 1: Study area showing all the nesting sites of Chestnut-headed Bee-eaters found during the study period

solitary nesters (Hoi and Hoi-Leitner 1997). Since morphometric characters reflect the physical condition and the age of the individual, they provide insights into the composition of birds in colony and solitary nest sites.

Chestnut-headed Bee-eaters *Merops leschenaulti* (CHB) are tropical Old World birds (Family Meropidae) that breed both solitarily and in small colonies of 4-8 breeding pairs. Occasionally, large colonies of hundreds of nests have been found (Grimmett *et al.* 1998). CHBs nest in horizontal tunnels up to 2 m long that they dig in sandy banks of streams or on level sandy ground (Ali and Ripley 1970) and on the mudbanks created by road construction. As bee-eaters show wide variation in their social and breeding organisation (Fry 1972), they are appropriate models to investigate how colony formation is influenced by the availability of nesting habitat. A study on colonial breeding in European Bee-eater *Merops apiaster* found a negative relationship between reproductive success and colony size, and suggested that some resource constraints may be responsible for colonial behaviour in their study population (Hoi *et al.* 2002). In the Blue-tailed Bee-eaters *Merops philippinus* breeding in Kinmen Islands, it was observed that many suitable sites were not used and at certain

sites, there was high level of clumping (Yuan *et al.* 2006). However, in a recent study, it was found that increasing the amount of substrate available at a nest-site led to an increase in breeding density (Wang *et al.* 2009). Therefore, the evidence for the role of habitat availability in influencing colony sizes is equivocal and studies on related species with varying degrees of social organization will help us understand the trade-off between habitat availability and conspecific attraction in nest-site selection. This study is an attempt to understand the influence of nesting habitat availability, and examine the composition of colonial and solitary nesting CHB, using their morphometric measurements.

STUDY AREA AND METHODS

The field work was carried out from December 2010 to May 2011, in Haliyal and Karwar Forest Division in Uttara Kannada district, Karnataka (Fig. 1). A total of 17 nests were found during the course of the study. The study area is part of the Western Ghats, with altitude 500-600 m above msl. Soil is deep and loamy, and the forest type is moist deciduous dominated by teak (Champion and Seth 1968).

Table 1: Comparison of habitat characteristics of solitary and colony nests of Chestnut-headed Bee-eaters in Haliyal and Karwar forest divisions, Karnataka (December 2010 to May 2011)

Habitat Characteristic	Colony (n = 12)		Solitary (n = 5)	
	Mean (S.D.)	Mean (S.D.)	Mean (S.D.)	Mean (S.D.)
Soil penetrability (1-20)	10.58 (3.60)	11.10 (4.04)		
Slope (in degrees)	70.00 (8.79)	73.00 (7.58)		
% Ground vegetation cover	14.17 (19.05)	5.00 (11.18)		
Distance to nearest used perch (m)*	2.26 (1.23)	6.43 (2.04)		
Height of embankment (m)	2.06 (52.28)	1.72 (1.13)		
Height of nest (m)	1.39 (0.63)	1.31 (1.46)		

* Mann-Whitney U Test: $U = 5.00$, $N1=12$, $N2=5$, one-tailed $P = 0.004$

Local birdwatchers were contacted and information on foraging sites, breeding season and nesting sites of CHB was gathered. Each potential nesting site was visited and checked for evidence of nesting in previous years, and for presence of foraging CHBs. Sites fulfilling either of these conditions were then visited repeatedly to check for CHB breeding activity. Roughly 100 hours were spent searching for nests. There were three colonies (two colonies with three nests each, one with six nests) and five solitary nests (Fig. 1). The maximum distance between two nests in a colony was c. 65 m. The maximum 'nearest neighbour distance' for a colony nest was about 34 m and the minimum 'nearest neighbour distance' for a solitary nest was greater than 700 m. The nearest distance between the two colonies was 4,290 m; between solitary nests was 1,139 m; and between a solitary nest and a colony was 723 m. Nests found in this study were located in abandoned mine sites, road banks and sandy banks of the backwaters of a dam.

Based on previous studies on breeding biology and nest site-selection in bee-eaters, the following variables were measured to characterise habitat quality: (i) soil penetrability was measured using a Lang Penetrometer which expresses resistance to penetration in pounds on a scale reading from one to twenty; (ii) slope of the embankment was measured using a plumb line extending from a protractor held inverted; the base of the protractor was aligned parallel to the substrate, the reading to the nearest degree against the plumb line measured the inclination of the embankment; (iii) percent vegetation cover was visually estimated in 0.5 m radius around the nest tunnel entrance; (iv) distance to the nearest used perch was measured with a measuring tape; (v) height of embankment was measured using a Tandem Clinometer cum compass; (vi) bearing of nest tunnel was measured using a

compass; (vii) distance of nesting site to the nearest water source was either visually estimated (when the site was adjacent to a water body) or measured using Google Earth™ (Asokan *et al.* 2009; Boland 2004; Heneberg 2009; Yuan *et al.* 2006).

Nesting habitat available was measured using Google Earth™ for nesting sites in abandoned mine sites. For nesting sites on linear structures like roads and banks, nesting area available was obtained by multiplying the length of the continuous stretch having similar vegetation characteristics with the average height of the road cutting.

Eighteen CHBs were captured using mist nets spread over the nest tunnel entrance in the early morning hours (6:00-7:00 hrs) and banded using numbered aluminium rings provided by the Bombay Natural History Society, Mumbai (Appendix 1). Morphometric measurements of bill and tarsus were made using dial vernier callipers (least count: 0.01 mm). Tail length and wing length was measured using a graduated scale and measurements were made to the nearest millimetre. The weight of the birds were measured using a 50 gm spring balance to the nearest 0.1 gm. The techniques detailed in the North American Banders' Manual were followed during capture, banding and measuring (North American Banding Council 2001).

As the sample size was low, we used non-parametric statistical tests. One-tailed Mann-Whitney U-test was used to test whether habitat quality was better at colony nesting sites than at solitary nesting sites. Two-tailed Mann-Whitney U-test was used to test differences in morphological measurements of CHBs in solitary and colonial nesting sites (Siegel and Castellan 1988). All analyses were done using SPSS 16.0 (Norussis 1992).

RESULTS

Mann-Whitney U-test results showed that distance to nearest used perch was significantly greater for solitary nests than colony nests (Table 1). Distance to nearest water source for the three colony sites was 10 m (Hudsa colony), 620 m (Jungle Lodges colony) and 760 m (Bison mine site colony). The mean and standard deviation of bearing of the nest tunnels was 183.64 ± 104.25 degrees, $n = 17$ [$n =$ No. of nests]. Amount of substrate available for the birds showed large variation. The maximum nest density was in Jungle Lodges colony that had three nests in 50 sq. m, the minimum nest density was in Hudsa with three nests in 1,11,840 sq. m. There were a few sites that were apparently suitable for breeding (small openings in the forest with plenty of breeding substrate available) but were not used by CHBs in the study season.

Among the morphological features, only tarsus length differed significantly between colony nesters and solitary nesters (Table 2). The standard deviation in weight, wing length, bill length and tail length was greater in colony nesters than in solitary nesters. Tarsus length and bill depth did not show much difference in standard deviation when compared across solitary and colonial nesters.

DISCUSSION

Though the sample size of the study is too low to make broad inferences, the results may suggest that colony formation was not influenced by either habitat quality or abundance. Among all the variables measured that characterised the quality of the habitat, only distance to nearest used perch site was significantly greater for solitary nesters than for colonial nesters. However, this difference seems to be an outcome of colonial nesting rather than the cause, as there were other perches available in the areas with solitary nests that could have been used by the bird. One possible reason for this difference could be that the individuals nesting solitarily guard the nest from a greater distance to reduce the chances of being noticed by a predator. Avoiding the nest and staying inconspicuous has been observed to be a nest defence strategy in many bird species (Burhans 2000; McLean 1987). However, the colony nests were conspicuous, so guarding a nest from a distance was probably not advantageous.

The large variation in the ratio of number of nests in an area to the amount of substrate available suggests that sites for nesting were not limiting in the study area. This contrasts with the finding in Rainbow Bee-eater *Merops ornatus*, where the number of nests in a colony was found to be tightly correlated with the amount of cleared ground cover available for nesting (Boland 2004). Even in Blue-tailed Bee-eaters, experimental increase in substrate available resulted in increase in nest density (Wang *et al.* 2009)

One important habitat variable that could not be measured in this study is aerial insect availability. Insect distribution and abundance is influenced by land-use heterogeneity and proximity to water (Brown *et al.* 2002). Both these factors were uniform in all the breeding sites in the study area, and hence, we assumed that the insect availability should be similar in all nesting sites. However, future studies should empirically verify this assumption.

Differential colony size choice by different individuals can mask the influence of habitat in nest-site selection, especially in cases where despotism exists and larger individuals may drive smaller individuals to sub-optimal sites. Since tarsus length does not change after a bird reaches the fledging age, it is considered to be a good measure of body

Table 2: Morphometric differences between colony nesting and solitary nesting Chestnut-headed Bee-eaters in Haliyal and Karwar divisions, Karnataka

Morphological feature	Colony (n = 13)	Solitary (n = 4)
	Mean (S.D.)	Mean (S.D.)
Weight (gm)#	27.64 (3.23)	25.75 (1.26)
Wing length (mm)	109.54 (3.15)	110.00 (1.15)
Bill length (mm)	32.34 (1.98)	32.42 (2.99)
Bill depth (mm)	5.66 (0.68)	5.44 (0.76)
Tarsus length (mm)*	14.05 (1.41)	12.02 (1.31)
Tail length (mm)	75.00 (3.65)	73.75 (1.26)

#n=14, for colonial nesters

*Mann-Whitney U Test: $U = 8.00$, $n_1 = 13$, $n_2 = 4$, 2-tailed $p = 0.045$

size (Freeman and Jackson 1990). The mean tarsus length was found to be different in colonial nesters and solitary nesters; the colonial nesters being marginally larger. Also, a number of instances of aerial chases were observed in the beginning of the breeding season when nest building had just been initiated, suggesting despotism.

Morphometric variables that are prone to change after fledging (i.e., wing length, tail length, weight) were found to have greater variation among colonial than solitary nesters (Table 1). One plausible explanation for this is that a colony comprises a population belonging to different age-classes, while individuals of a particular age-class (the age class that is nearest to the population mean) constitute the population that made solitary nests. In White-fronted Bee-eaters *Merops bullockoides* extended family units each consisting of a multi-generation lineage coexisted and formed colonies (Emlen and Wrege 1988). In European bee-eater, breeding among close relatives from different generations has been reported (Lessells *et al.* 1994). The evidence from this study suggests that in CHBs also colony nesters might belong to different age-cohorts probably comprised of related individuals. In a scenario where colonies are formed by related individuals who exclude other individuals from occupying the nest-site, the utilisation of nesting sites need not be in proportion to the habitat available to them.

The choice of nest sites observed in our study population was similar to that found by Yuan *et al.* (2006) in Blue-tailed Bee-eaters, where several suitable nesting sites were not utilised. Unlike in the European Bee-eater (*Merops apiaster*) population studied by Hoi *et al.* (2002), habitat constraints did not drive colony formation in our study population of CHBs. Since the hypothesis that the colonies are formed either due to variation in habitat quantity and/or

quality was not supported through this study, the alternative explanation that social benefits might be influencing colony formation in this species, needs to be tested (Alexander 1974; Richner and Heeb 1996; Safran *et al.* 2007).

Thus, colony formation in CHBs may be driven by conspecific attraction and not by habitat-mediated aggregation. Among the conspecific attraction hypotheses, only the traditional aggregation hypothesis and conspecific reproductive hypothesis are likely to apply to bee-eaters. Since, bee-eaters are mostly monogamous and the rate of extra-pair copulation is also low (Fry *et al.* 1992), the hidden-lek hypothesis of colony formation is ruled out. Conspecific reproductive success hypothesis assumes that reproductive success varies across different sites (Danchin *et al.* 1998). In this study population, reproductive success was not found to vary among breeding sites (own published data) and hence conspecific reproductive success could not have acted as a cue for selection of breeding sites. Thus, traditional aggregation seems to be responsible for colony formation in CHBs. The role of previous years' nesting holes (evidence of former presence of conspecifics) as a cue needs to be further examined. All three colony sites and two of the five solitary nests had nest tunnels from previous breeding seasons. Other studies have also reported presence of previous years' nest tunnels at breeding sites in many species of bee-eaters (Burt

2002; Fry *et al.* 1992). The presence of former nesting tunnels in breeding sites could also be attributed to site fidelity shown by bee-eaters. During the study, in two separate instances a breeding pair dug a nest in heap of sand meant for construction work. This offers evidence against the role of site fidelity by CHBs at least for solitary nesters.

Future studies directed at testing the various conspecific attraction hypotheses in CHBs may yield more insights into the evolution of colonial breeding in birds.

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For Appendix 1, see page 36

Appendix 1: Ring numbers and measurements of all the captured birds

Species	Weight (gm)	Age	Moult	Plumage	Broad	Wing length (mm)	Bill length (mm)	Bill depth (mm)	Tarsus length (mm)	Tail (mm)	Locality	Habitat	Date
AB168951	29	5	1	4	2	107	33.75	6.62	12.92	77	1	1	01-03-2011
AB168952	25	5	1	4	2	109	31.23	5.18	15.14	75	2	2	02-03-2011
No ring	25	5	1	4	2						2	2	02-03-2011
AB168953	27	5	1	4	2	110	32.76	4.88	14.81	73	1	1	04-03-2011
AB168954											3	3	04-03-2011
AB168955	30	5	1	4	2	109	34.35	6.41	16.2	70	2	2	05-03-2011
AB168956	28	5	1	4	2	112	31.42	6.45	14.54	76	2	2	05-03-2011
AB168957	25	5	1	4	2	110	32.77	6.35	13.45	69	2	2	05-03-2011
AB168958	23	5	1	4	2	111	34.47	5.18	14.91	75	2	2	05-03-2011
AB168959	31	5	1	4	2	108	34.44	5.5	12.78	77	2	2	29-03-2011
AB168960	36	5	1	4	2	111	34.48	6.42	11.32	79	1	2	30-03-2011
AB168961	27	5	1	4	2	117	31.25	5.26	15.1	82	2	2	08-04-2011
AB168962	26	5	1	4	2	110	30.11	4.78	14.63	77	2	2	08-04-2011
AB168963	28	5	2	2	2	106	28.11	5.15	12.1	71	1	1	09-04-2011
AB168964	27	5	1	4	2	104	31.27	5.34	14.72	74	1	1	18-04-2011
AB168965	19	5	1	4	2	93	29.47	4.82	10.15	103	4	2	23-04-2011
AB168966	24	5	1	4	2	111	36.8	5.6	13.22	74	5	2	27-04-2011
AB168967	27	5	1	4	2	111	31.45	6.44	12.88	75	6	2	03-05-2011
AB168968	26	5	1	4	2	109	31.42	4.86	11.63	74	7	2	04-05-2011
AB168969	26	5	1	4	2	109	30.02	4.84	10.34	72	8	2	05-05-2011

Age: 1 - Nestling, 2 - Juvenile (first year); 3 - Sub-adult; 4 - Immature; 5 - Adult; 6 - Fullgrown but stage unknown

Moult: 1 - No moult; 2 - Wing moult; 3 - Tail moult; 4 - Wing and tail; 5 - Head; 6 - Body; 7 - Head and body; 8 - General moult

Plumage: 1 - Down; 2 - Juvenile (first year); 3 - Intermediate; 4 - Adult; 5 - Eclipse; 6 - Breeding; 7 - Partial breeding

Broad patch: 1 - absent; 2 - present but details not recorded; 3 - Skin smooth, glossy, free of feathers; 4 - Skin smooth, network of blood vessels noticeable; 5 - Skin thickened, blood vessels not noticeable, fluid layer under epidermis, broad patch resembles a second degree burn; 6 - Skin wrinkled, dried up, begins to form scales; 7 - Skin becomes smooth, feather calami formed, broad patch begins to be covered up

Locality: 1 - Junglic Lodges colony, 2 - Bison mine site colony, 3 - KPC colony, Ganeshgudi, 4 - Kodapani watchtower, 5 - Kodli roadside, 6 - Right Bank, 7 - Nagoda, 8 - Rafting jetty mine site

Habitat: 1 - Edge of moist deciduous forest; 2 - Moist deciduous forest